

Limnology of the southern acid peat flats, South-western Australia

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Abstract

Temporal changes in water chemistry and invertebrate community composition, abundance and diversity were monitored for two years and one year, respectively, for aquatic habitats in an extensive area of coastal wetlands of South-western Australia. The locations sampled included permanent and temporary lotic and lentic environments. pH was low and declined to a minimum of 4.1 in winter. Water transparency was also low due to high levels of dissolved organic substances. A distinct effect of season on water chemistry was observed in contrast to changes reported for other small Australian ponds, temporary or otherwise. Significant temporal changes in the density, diversity and composition of the invertebrate fauna (zooplankton and zoobenthos) were recorded. Fish predation was potentially an important determinant of invertebrate diversity and community structure. Few of the insect fauna showed adaptations to ephemerality and fauna known to be associated with temporary waters were, in general, lacking. This is suggested to be due to the predictable seasonality of the climate which allows little distinction between temporary and permanent habitats for a highly seasonal fauna. Similarity of species composition between locations was low for insect fauna, reflecting the lack of specific drought survival mechanisms and the importance of opportunism and colonization ability. Assemblage similarity was greatest for the crustacean fauna and was attributed to a greater prevalence of drought survival mechanisms.

Introduction

The seasonal nature of much of Australia's rainfall has ensured that many aquatic habitats are temporary in nature. Limnological studies of Australian temporary water bodies have encompassed pools (Edward 1964, Jones 1974, 1975, Bayly 1982), ponds (Morton & Bayly 1977), streams (Towns 1985, Bunn *et al* 1986, Boulton & Suter 1986, Smith & Pearson 1987) and lakes (Bonython & Mason 1953, Maher 1984, Maher & Carpenter 1984). Notwithstanding the above, temporary waters are among the least studied of Australian standing waters (Bayly & Williams 1973).

Although the presence of temporary aquatic habitats is usually seasonally determined, this is less so for the variations in physico-chemical parameters. Ponds, temporary or otherwise, are said to be characterized by their high degree of physico-chemical and biological variability (Bayly & Williams 1973, Williams 1980). For example, Bayly & Williams (1973) suggest that seasonal patterns of oxygen concentration and pH in shallow ponds are absent or ill-defined. This was shown to be the case for fluctuations in conductivity in south-eastern Australian temporary ponds (Morton & Bayly 1977) and Timms (1967, 1970a, b) showed variation in total dissolved solids and major ions of a number of permanent ponds to be

highly variable and related to aseasonal rainfall. Similarly, Towns (1985) and Smith & Pearson (1987) present data that show, for pools in temporary streams, that changes in water chemistry were erratic, showed no seasonality, and in the latter study, were most greatly influenced by unpredictable rainfall. Such a relationship between aseasonal variation in chemical parameters and rainfall is not unexpected for areas where the pattern and the amount of rainfall is unpredictable (McMahon 1982, Lake *et al* 1986). In contrast, a Western Australian temporary stream showed a distinct seasonal pattern of variation in all parameters measured (Bunn *et al* 1986). These authors stress the importance of the predictability and regular seasonality of the region's climate to stream water chemistry and macro-invertebrate community structure.

Some biological features of Australian temporary aquatic habitats have been detailed (*eg* Bayly & Williams 1973) but apply only in the general sense. They generally have fewer species than permanent ponds and temporary streams (Bunn *et al* 1986, Boulton & Suter 1986) and pools in intermittent streams (Towns 1985, Smith & Pearson 1987). Temporary waters are suggested to provide habitats where competition between species is of little importance in determining patterns of distribution because of insufficient time for completion of competitive exclusion (Bayly & Williams 1973, but see Morton & Bayly

1977). Differences in species richness and composition between areas are most likely a result of colonization probabilities and geographical proximity.

Our study investigated the limnology of a range of lotic and lentic temporary and permanent water bodies of the southern acid peat flats of South-western Australia. A major aim was to determine the importance of the reported seasonality of the climate (Bunn *et al* 1986) on the physical and chemical environment and invertebrate community.

Methods

Study area

The study area was located in the south-west of Western Australia (Fig. 1). This area has a Mediterranean climate with high winter rainfall and dry hot summers. Tall dense forests of karri (*Eucalyptus diversicolor*) and jarrah (*E. marginata*) are typical of the area. In coastal areas the

forests give way to low-lying heath and sedgeland (Smith 1972). The transition from forest to heath may be dramatic, occurring over distances of less than 100m and corresponding to an abrupt change from red erosional soils to leached peaty sands of the Chudalup and Blackwater associations (McArthur & Clifton 1975).

The localities sampled in this study include a range of habitats from temporary to permanent pool (sites 2, 3, 8 & 9 and sites 1 & 6 respectively) and temporary to permanent stream (sites 5 & 4 respectively). Within the pool category, both sites 1 & 9 were drained by a temporary stream. Site 8 was fed by a short (200 m) shallow stream. The physical characteristics of the study sites are further described in Pusey & Edward (1990). Site numbers used in that report are maintained here. Temporary water sites contained water from late autumn to mid-summer. All sites were either located in broad shallow valleys of the southern acid peat flats (Christensen 1982) or fed by drainage from such areas.

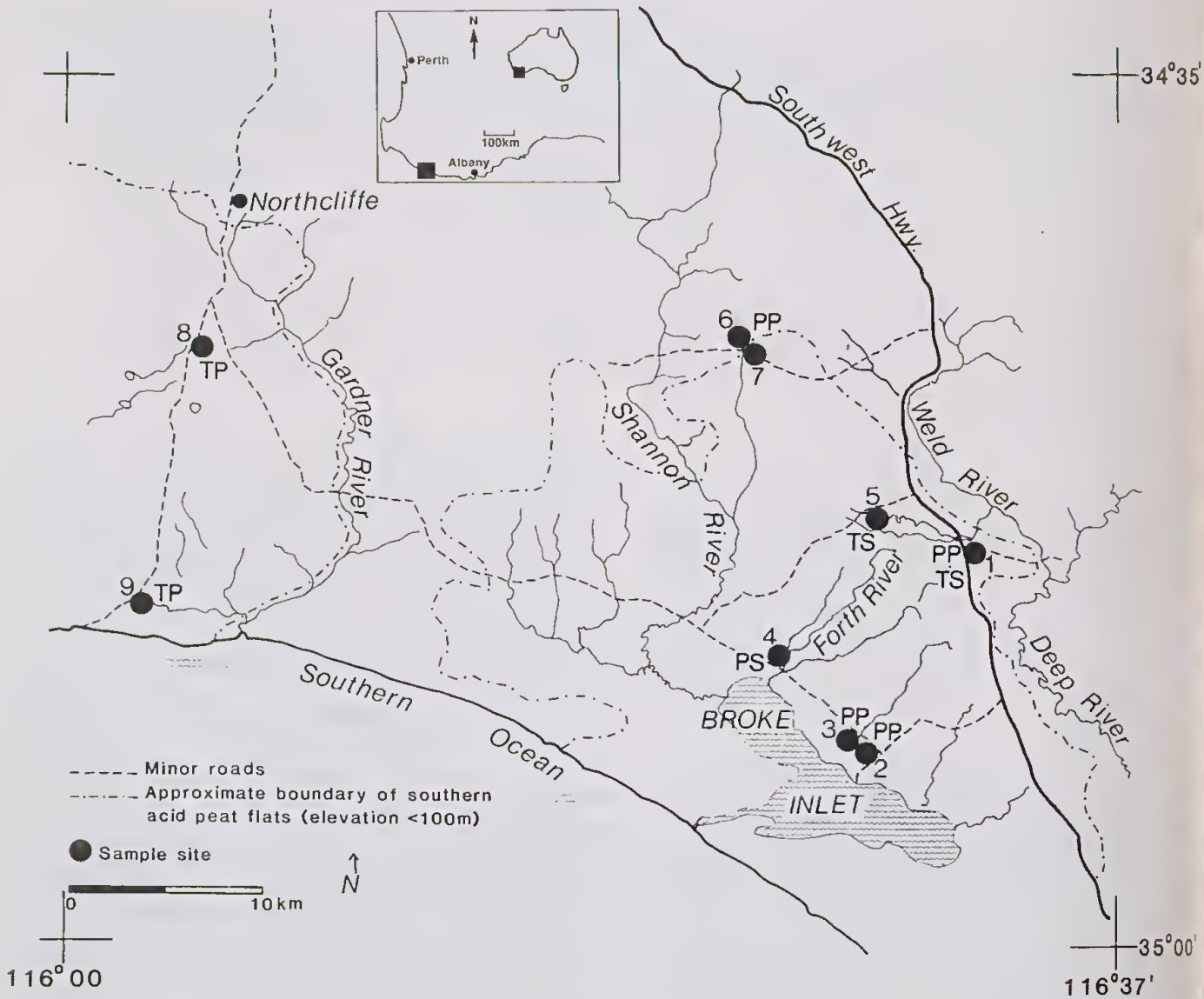


Figure 1 Location of the study sites and the approximate boundary of the southern acid peat flats. TP = temporary pool, TS = temporary stream, PP = permanent pool, PS = permanent stream.

Water chemistry

A single water sample was taken from the centre of each water body on each sampling occasion, immediately placed on ice and returned to the laboratory. Cation (Na^+ , K^+ , Ca^{2+} & Mg^{2+}) concentrations were determined by atomic absorption spectrophotometry (Varian AA475) and pH on a Chemtrix type 40 meter. Chloride ion concentrations were measured on a Buchler Cotlove (4-2000) chloridometer. Water temperatures were measured on each sampling occasion with a mercury thermometer. Dissolved oxygen concentrations were measured by a Delta Scientific model 1010 oxygen probe.

Optical clarity of the water was determined for four of the eight sites (1, 2, 4 & 6). Four replicate water samples were taken from each site in early June 1987 and kept on ice for 24 hours. A Secchi disc depth and one water sample were taken from the Deep River to provide a comparison as shallow water depths precluded the use of a Secchi disc at the study sites. Between 100 and 200 ml of each water sample were filtered through 0.45 μm Millipore filters and the absorbance at 440nm of the filtrate determined in a Beckman Model 25 spectrophotometer and expressed as the G440 (*sensu* Kirk 1976).

Chlorophyll concentrations were determined for each of the four sites above by the method of Strickland and Parsons (1968) using a Beckman model spectrophotometer. Total chlorophyll concentration (a, b & c) was estimated from the absorption spectrum of the supernatant resulting from the analysis detailed above.

Substrate particle size distribution

Four replicate substrate cores (10 cm diameter, 10 cm deep) were taken from each site. Each core was dried at 30°C until a constant weight was obtained. Organic material was separated from the inorganic fraction by flotation. Both fractions were again dried to a constant weight and the mean organic content estimated. The organic component was divided into two fractions: coarse particulate organic matter (CPOM—particles of a diameter equal to or greater than 1 mm) and fine particulate organic matter (FPOM—particles of a diameter less than 1 mm). The size distribution of the inorganic particles was estimated by sieving through a series of graduated sieves (8, 4, 2, 1, 0.5 & 0.25 mm).

The invertebrate fauna

The invertebrate fauna was sampled at each of the 8 locations on 5 occasions: twice before the summer drought of 1985/86 (Sep & Nov 1985) and 3 times after the beginning of the winter wet period (June, Aug & Sep 1986). Sampling in 1986 resumed within 3 wks of inundation of the sites. Plankton was collected by straining 45 l of water through a 0.25 mm sieve and the retained animals preserved in 70% alcohol. Three replicates were taken from each site. Benthic invertebrates were sampled with a 10 cm diameter core sampler. Three 10 cm deep sediment cores were taken from each site and immediately preserved in 10% formalin. Benthic organisms and organic material were later floated away from the inorganic fraction by immersion in a concentrated CaCl_2 solution. Both planktonic and benthic fractions were sorted under a stereomicroscope at 12X. All animals, with the exception of nematodes, were enumerated and

identified by matching against voucher specimens held in the Aquatic Research Laboratory, Department of Zoology, UWA. Abundances were expressed as the number of individuals $\cdot \text{m}^{-3}$ and m^{-2} for zooplankton and zoobenthos respectively.

Changes in abundance were assessed by a non-parametric two-way (site by time) analysis of variance by ranks. A non-parametric analysis was used because heteroscedasticity could not be reduced below significant levels by commonly employed transformations. Differences between means were tested with a non-parametric Tukey-type multiple comparisons test (Zar 1984: 199-201). Changes in diversity (estimated by the Shannon index) were analysed the same way. Categories used in the estimation of diversity are listed in the caption to Figure 6.

Results*Water chemistry*

Ionic concentrations varied seasonally and peak concentrations were achieved in or just prior to summer when water volumes were at their minimum (Fig. 2). The concentration of dissolved salts was low at all sites and Na^+ was the dominant cation, usually followed by Mg^{2+} , Ca^{2+} and K^+ . Except at site 9, K^+ was occasionally more concentrated than Ca^{2+} while at this site (9), Ca^{2+} was often more concentrated than Mg^{2+} . The mean (\pm SE) proportion of total measured cations contributed by Na^+ was high; $84.2 \pm 1.2\%$.

H^+ concentration also varied seasonally with pH at its minimum in mid winter. Sites 2 & 3 were the least acidic and pH was never recorded below 5.0 at these sites. A minimum pH of 4.1 was recorded at Sites 5 & 8. No consistent relationship between Ca^{2+} and pH was apparent within any one site but sites with the highest pH tended to have elevated calcium concentrations (Sites 2, 3 & 9).

Oxygen concentration and water temperature also showed seasonal variation in magnitude. Similar temperatures were recorded for each site with maximum temperatures being recorded in or just prior to summer (Table 1). Maximum dissolved oxygen concentrations were recorded during the winter months when temperatures were at their lowest. Although dissolved oxygen was lowest in summer at no time was it observed to fall below 50% saturation.

Optical clarity varied between sites (Table 2). Site 1, with a G(440) of 3.58 m^{-1} , contained the darkest water and absorbance was equivalent to that of the Deep River where a Secchi disc depth of 1.1 m was recorded. Sites 3 and 6 had low absorbance values and were virtually colourless. Of the sites not sampled in this analysis, all except Site 2 were darkly stained and 'tea-coloured'. Chlorophyll (a, b & c) concentration was not negatively associated with water clarity as the highest concentration occurred in the darker water site (Table 2). Although planktonic algae were at low density at Site 3 it was noticed at the time of sampling that the substrate was covered by a fine mat of filamentous algae. This was also observed at Site 2 but at no other site during the period of study. Low chlorophyll concentrations were recorded from the running water site, Site 4.

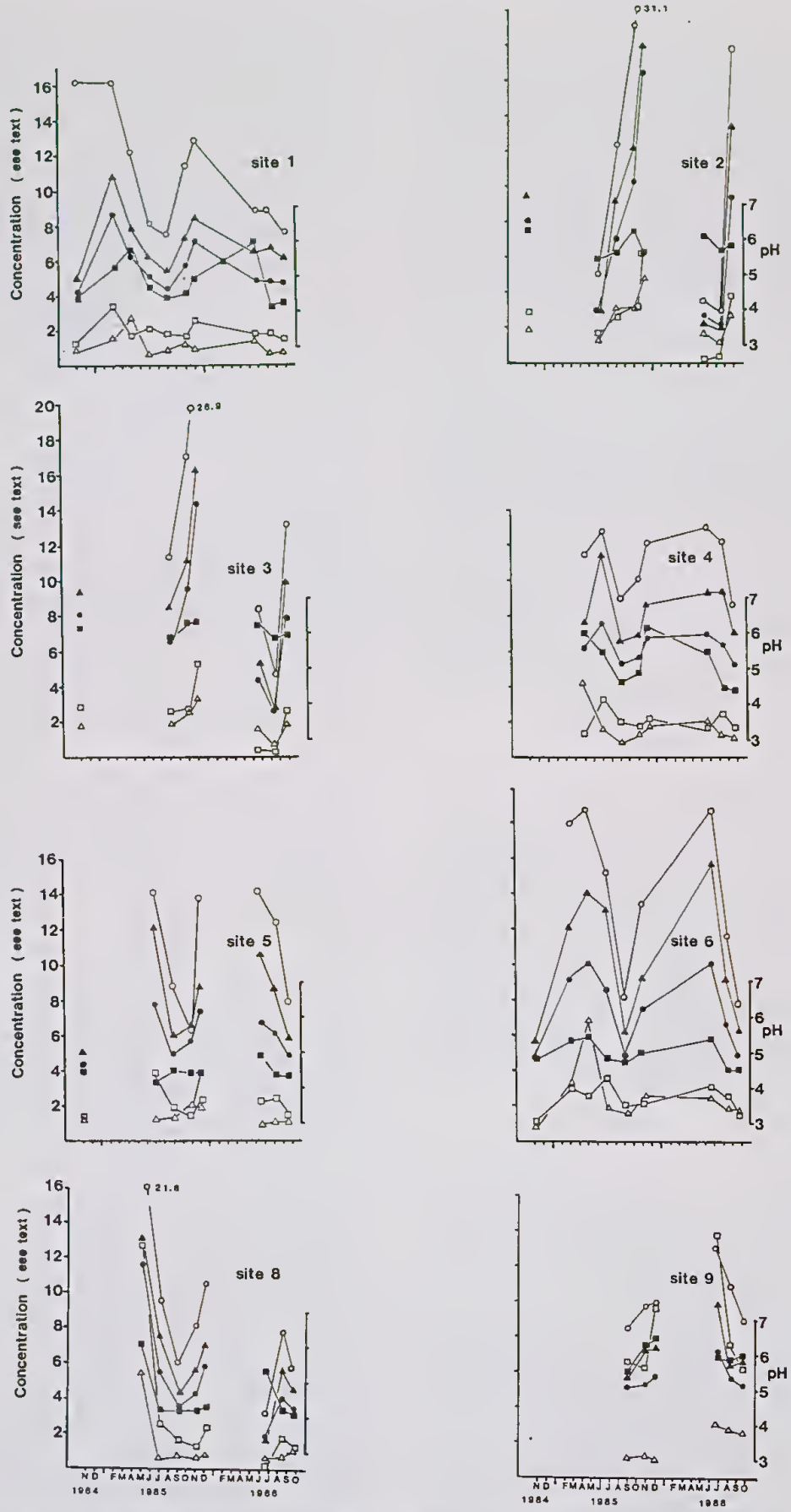


Figure 2 Temporal changes in the concentration of major ions and pH at each of the study sites. Concentrations are given as ppm except for Na^+ and Cl^- where concentrations are expressed as $\text{ppm} \times 10^{-1}$. $\circ = \text{Cl}^-$, $\bullet = \text{Na}^+$, $\square = \text{Ca}^{2+}$, $\blacksquare = \text{pH}$, $\triangle = \text{K}^+$ and $\blacktriangle = \text{Mg}^{2+}$

Table 1

Maxima and minima water temperatures and oxygen concentrations for each site. The month in which the measurement was made is given in parentheses. (- denotes no measurement was made).

Site	Temperature		Dissolved Oxygen Concentration (ppm)	
	Max	Min	Max	Min
1	25.2 (Dec)	7.6 (June)	8.4 (June)	5.9 (Dec)
2	24.0 (Nov)	10.2 (Aug)	10.0 (June)	7.9 (Nov)
3	25.8 (Nov)	8.0 (Sept)	10.0 (June)	—
4	23.5 (Feb)	9.7 (June)	8.8 (June)	7.7 (Dec)
5	25.0 (Nov)	11.6 (June)	—	5.2 (Dec)
6	22.0 (Feb)	5.1 (June)	8.0 (June)	5.6 (Nov)
8	26.0 (Nov)	13.0 (Aug)	—	8.1 (Dec)
9	28.0 (Nov)	12.0 (Aug)	—	8.0 (Dec)

Table 2

Gilvin absorption (G440) and chlorophyll concentration (a, b and c) (μgL^{-1}) at four of the study sites and the Deep River. The mean value and standard error are given with the number of replicates in parentheses.

Site	G440	Chlorophyll concentration
1	3.58±0.41 (4)	6.53±0.91 (4)
2	0.59±0.05 (4)	2.44±0.32 (3)
4	1.30±0.00 (4)	2.12±0.40 (4)
6	0.75±0.20 (4)	4.26±0.25 (3)
Deep River	3.60 (1)	4.44 (1)

Substrate particle size distribution

The organic content of the substrate differed between sites (Fig. 3). Sites 2, 3 & 4 contained very little organic matter with total organic content being less than 1% dry weight. Sites 1, 5, 8 & 9 all had a total organic content of between 1 and 5% dry weight. Site 6 had the greatest organic content, 38% dry weight. The contribution of CPOM to the total organic content was similar for all sites. The inorganic sediment was composed primarily of particles less than 1 nm diameter. Substrate particle size distribution appeared to be similar in all sites although this may be partly a reflection of the sieve sizes used; Sites 2 & 3 had clay-like substrates in contrast to the white sands of the other sites.

The invertebrate fauna

The mean density of zooplankton and benthos showed significant temporal variation during the period of study ($P < 0.01$ for both). Significant variation between sites was also detected ($P < 0.01$ and 0.001 respectively) (Table 3). Densities were generally higher in June, the beginning of the wet season (Fig. 4 and Table 4). The maximum zooplankton density occurred at Site 2 where a mean density of 38 000 individuals m^{-3} was recorded. High mean zoobenthos density (25 000 individuals m^{-2}) was recorded at this site and time also. High densities of zoobenthos were also recorded at Sites 4 & 6 where mean

densities of 24 000 and 25 000 individuals m^{-2} were recorded, respectively (Fig. 3).

In general, zooplankton tended to be most abundant at the temporary pool sites (Sites 2, 3, 8 & 9) and least so at the two stream sites (Sites 4 & 5) and Site 6. Zoobenthos, however, showed no such pattern and between site differences in density were much less pronounced (Table 4).

Significant temporal variation in the diversity of zooplankton and zoobenthos was also detected ($P < 0.01$ and 0.05 respectively, Table 3). In general the trend was for diversity to be lowest when densities were highest (Figs 4 & 5). Zooplankton, but not zoobenthos, diversity varied significantly between locations. Changes in the density of the two calanoid copepods appeared to be the major determinant of changes in zooplankton diversity and density (Fig. 6) at temporary pool and temporary stream/pool sites (1, 2, 3, 8 & 9). Calanoid density usually decreased toward summer except at Site 3 in 1986. Zooplankton, in general, were a very minor component of the fauna at Site 4 and comprised only about 3% of the total number of individuals. In contrast, site 5, also a lotic habitat, showed a much greater contribution by plank-

Table 3

H values and their associated levels of significance for two way ANOVAs by ranks for density and diversity of zooplankton and zoobenthos. (ns - $P > 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Variable	Component	Source of variation	df	H	P
Density	Zooplankton	Site	7	21.9	**
		Time	4	14.4	**
		Site X Time	28	26.6	ns
	Zoobenthos	Site	7	25.0	***
		Time	4	14.1	**
		Site X Time	28	31.2	ns
Diversity	Zooplankton	Site	7	24.3	***
		Time	4	14.0	**
		Site X Time	28	18.7	ns
	Zoobenthos	Site	7	12.2	ns
		Time	4	10.6	*
		Site X Time	28	38.8	ns

Table 4

Between site and season differences in density and diversity of zooplankton and benthos. Highest to lowest values are arrayed from left to right. Mean values not significantly different from another ($P < 0.05$) are joined by a solid line.

Variable	Component	Factor	
Density	Zooplankton	Site	<u>3 2 9 1 8 5 6 4</u>
		Time	<u>J A S86 N S85</u>
	Zoobenthos	Site	<u>6 4 3 8 2 9 5 1</u>
		Time	<u>J A S86 N S85</u>
Diversity	Zooplankton	Site	<u>9 5 6 8 4 1 2 3</u>
		Time	<u>S85 S86 A J N</u>
	Zoobenthos	Time	<u>S86 N A S85 J</u>

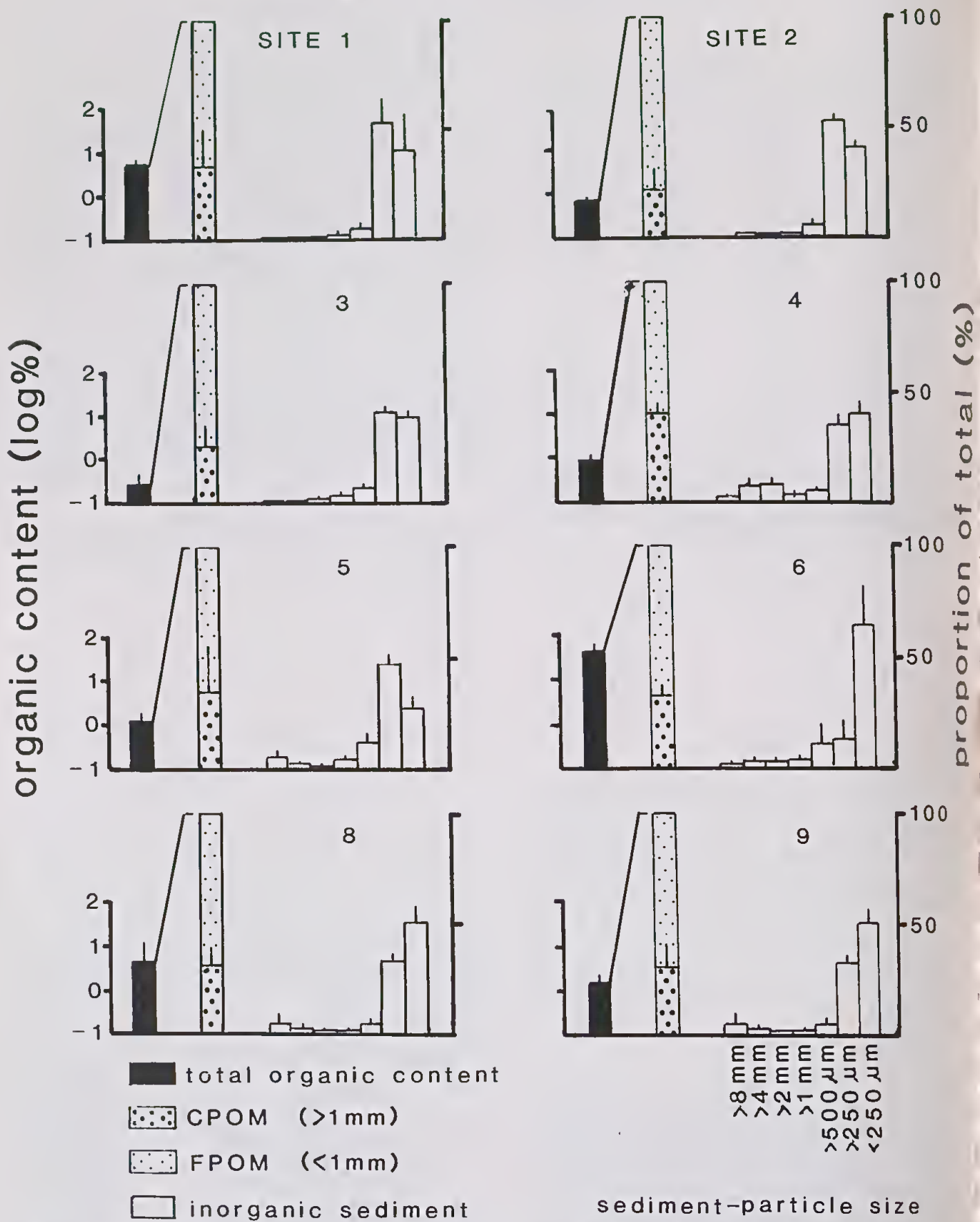


Figure 3 Proportion of organic sediment to the total sediment, the composition of organic sediment and the size distribution of inorganic sediment particles. (Note that the left hand axis is a log scale. CPOM and FPOM are coarse and fine particulate organic matter respectively. The mean and standard error of the mean from four replicate samples are shown.)

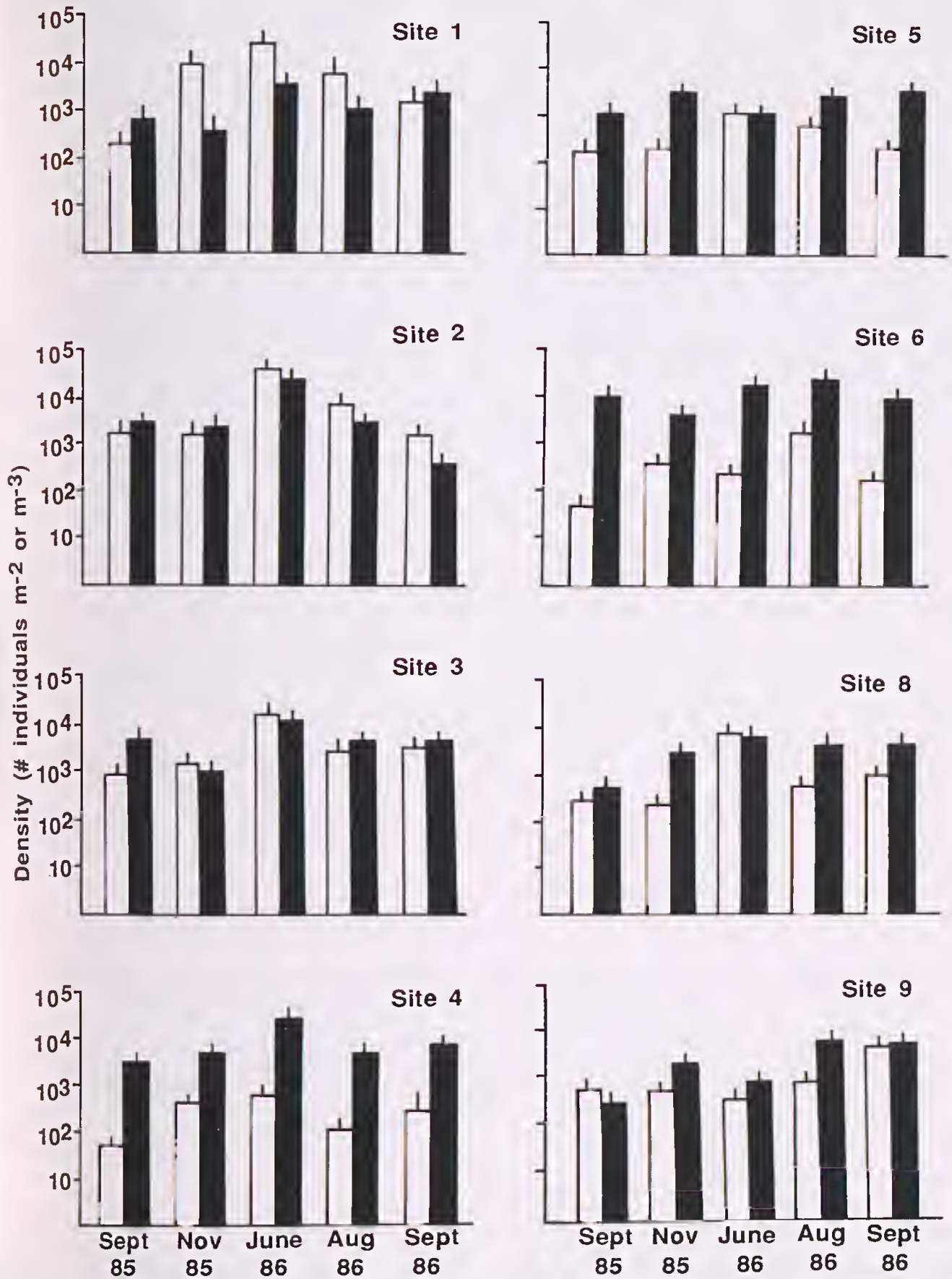


Figure 4 Temporal changes in the density of zooplankton and zoobenthos at each site during the study period. (Density is expressed as the number of individuals per cubic and squared metre respectively. The mean and SEM for three replicates are shown. Zooplankton is represented by the open bars and zoobenthos by the solid bars.)

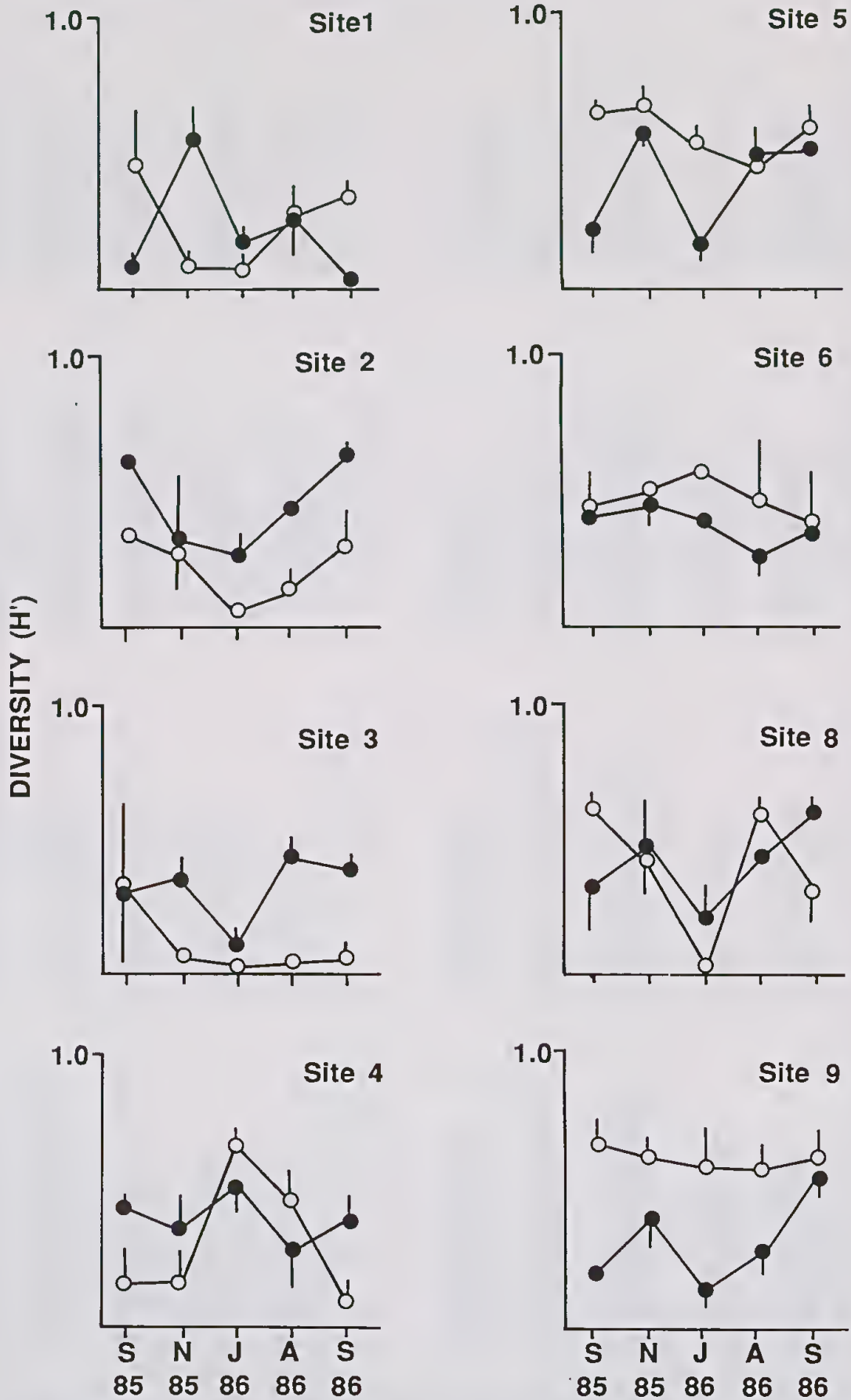


Figure 5 Temporal changes in diversity of zooplankton and zoobenthos at each site during the study period. (Mean & SE are shown. Shading is as in Fig. 4)

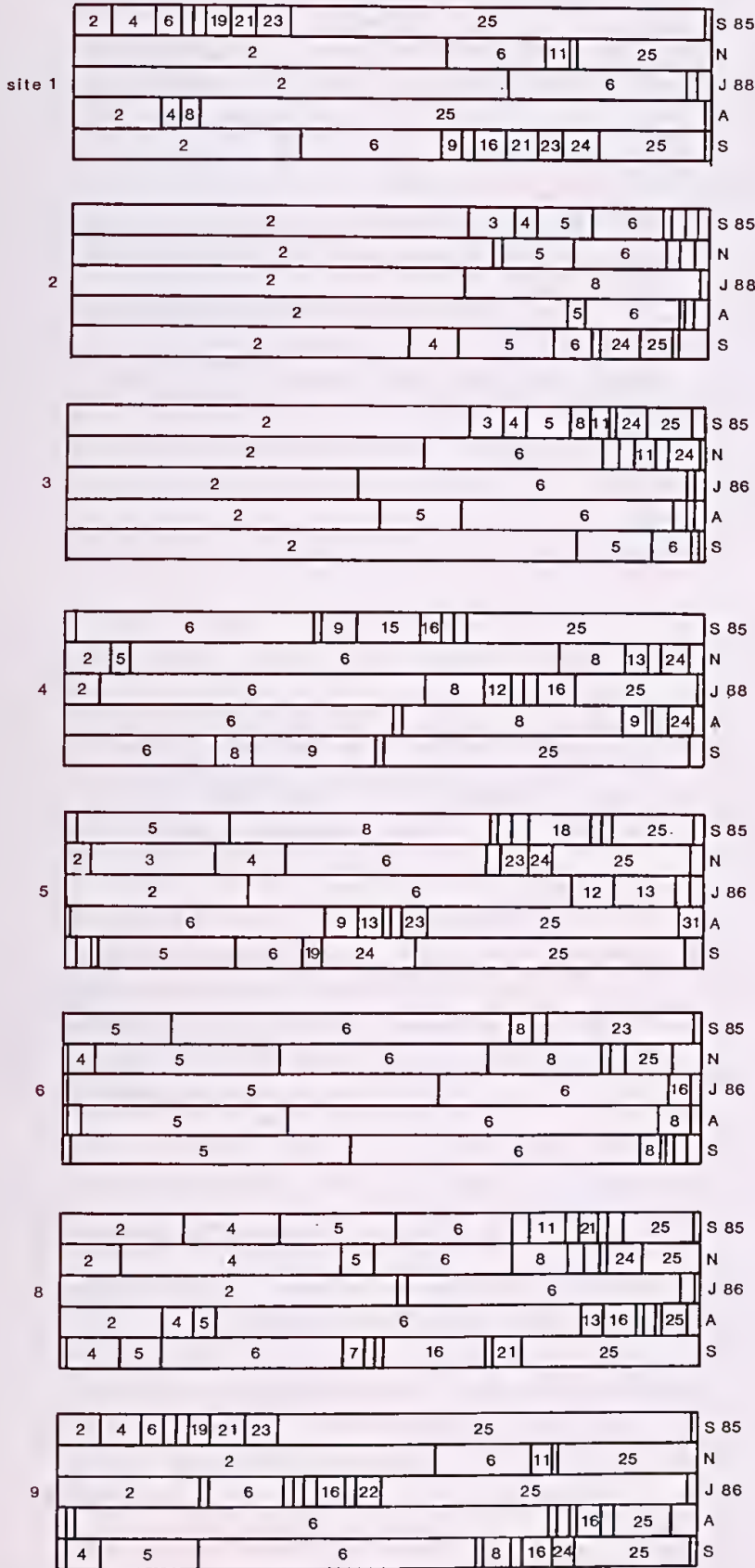


Figure 6 Temporal changes in the composition of the invertebrate fauna at each site. (Key to taxon code—
 2 Calanoidea 3 Harpacticoidea 4 Cladocera 5 Ostracoda 6 Chironomidae larvae 7 Chironomidae pupae 8 Ceratopogonidae larvae 9 Simuliidae larvae 10 Diptera adults 11 Coleoptera larvae 12 aquatic Coleoptera 13 Collembola 15 Plecoptera and Ephemeroptera 16 trichoptera 18 aquatic Hemiptera 19 other aquatic insect larvae 21 other terrestrial insects 23 Hydracarina 24 Amphipoda and Isopoda 25 Oligochaeta)

Table 5

Total number of taxa and number of taxa within major taxon groups present at each site.

	Total	Site							
		1	2	3	4	5	6	8	9
Total	135	42	41	40	58	44	46	43	50
Arachnida	11	0	2	1	0	4	6	0	5
Crustacea	26	12	17	16	9	14	10	14	11
Ostracoda	10	1	6	5	2	3	2	3	2
Copepoda	4	3	3	3	3	3	3	3	3
Cladocera	5	5	4	4	3	2	3	5	3
Insecta	94	30	28	22	47	25	28	28	34
Trichoptera	17	3	1	2	5	4	7	3	6
Coleoptera	12	1	7	5	2	3	2	3	2
Diptera	52	20	12	11	31	15	15	16	22
Chironomidae	38	17	10	9	23	10	12	16	17
Tanypodinae	5	3	4	1	3	0	4	4	2
Orthoclaadiinae	13	5	0	1	9	5	2	4	6
Chironominae	18	8	6	7	10	5	6	8	9
Aphroteniinae	2	1	0	0	1	0	0	0	0

tonic organisms, especially ostracods, to the total abundance. The stream at this site is much more intimately associated with the peat flats which form vast shallow areas of inundated sedgeland and from which nearly all the discharge of Site 5 originates. The flats undoubtedly contribute to the fauna of the stream.

Chironomid larva were an important component of the benthos at all sites except Site 1 and to a lesser extent Site 9 (Fig. 6). This group contributed greatly to the overall benthic density and changes in the density of chironomid larvae were largely responsible for observed seasonal changes in benthic density and diversity. The subfamily Chironominae numerically dominated the midge larva fauna of the pool sites (1, 2, 3, 6, 8 & 9) whilst the subfamily Orthoclaadiinae contributed greatest to abundance at stream sites (4 & 5) (Table 5 and Fig. 7). Those pool sites that were fed or drained by temporary streams also contained orthoclad larvae. In most cases, one species of chironomid larva was responsible for the majority of the total number of larvae present at a site at any given time (Fig. 7). At temporary pool sites 1, 2, 3 & 8, the dominant species was usually *Tanytarsus* sp 1. This species was also present at Site 9 where *Riethia* sp was also important. At the permanent pool site, Site 6, *Cladopelma curtiwalva* was the numerically dominant species although the tanypod, *Procladius* sp. was also common. *Stictocladus uniserialis*, an orthoclad, was the most abundant species at Site 4 and was also present at Site 5 but at lower densities. Diversity at Site 5 tended to be high and no single species was numerically dominant over the entire study period. Orthoclaadiinae tended to be the most abundant especially during periods of maximum flow. In November, when water levels were receding and flow decreasing larvae of the Chironominae were numerically important. The persistence of the composition of midge larval assemblages was low as almost 40% of all major (those contributing 5% or more to the total) species/site associations occurred in one of the two years. The majority of

those Chironomidae larvae achieving high densities could be assigned to the collector/gatherer trophic group and few scrapers or shredders were present (Table 6).

Of the 135 invertebrate taxa collected from the eight sites (Table 5 & Appendix 1) almost 70% were insects. The mean (\pm SE) proportion of insect taxa for temporary water

Table 6

Trophic status of major Chironomidae genera.

Only those species contributing >5% of the total number of individuals at any one site and time are included. Trophic status has been assigned according to Merritt & Cummins (1977) and Edward (unpublished data). The number of species within genera recorded in this study is listed in parentheses.

Species	Collector	Filter feeder	Scraper	Shredder	Predator
Tanypodinae					
<i>Procladius</i>					+
<i>Ablabesmyia</i>					+
Orthoclaadiinae					
<i>Stictocladus</i> (2)	+				
<i>Thienemanniella</i>	+				
<i>Limnophyes</i>	+				
<i>Parakiefferiella</i>	+				
Orthoclaadiinae sp (3)	+				
Chironominae					
<i>Cryptochironomus</i>	+				+
<i>Dicrotendipes</i> (2)	+		+		
<i>Cladopelma</i>	+				+
<i>Polypedilum</i>	+			+	
<i>Riethia</i>	+			+	
<i>Tanytarsus</i> (2)	+				
<i>Rheotanytarsus</i>	+	+			

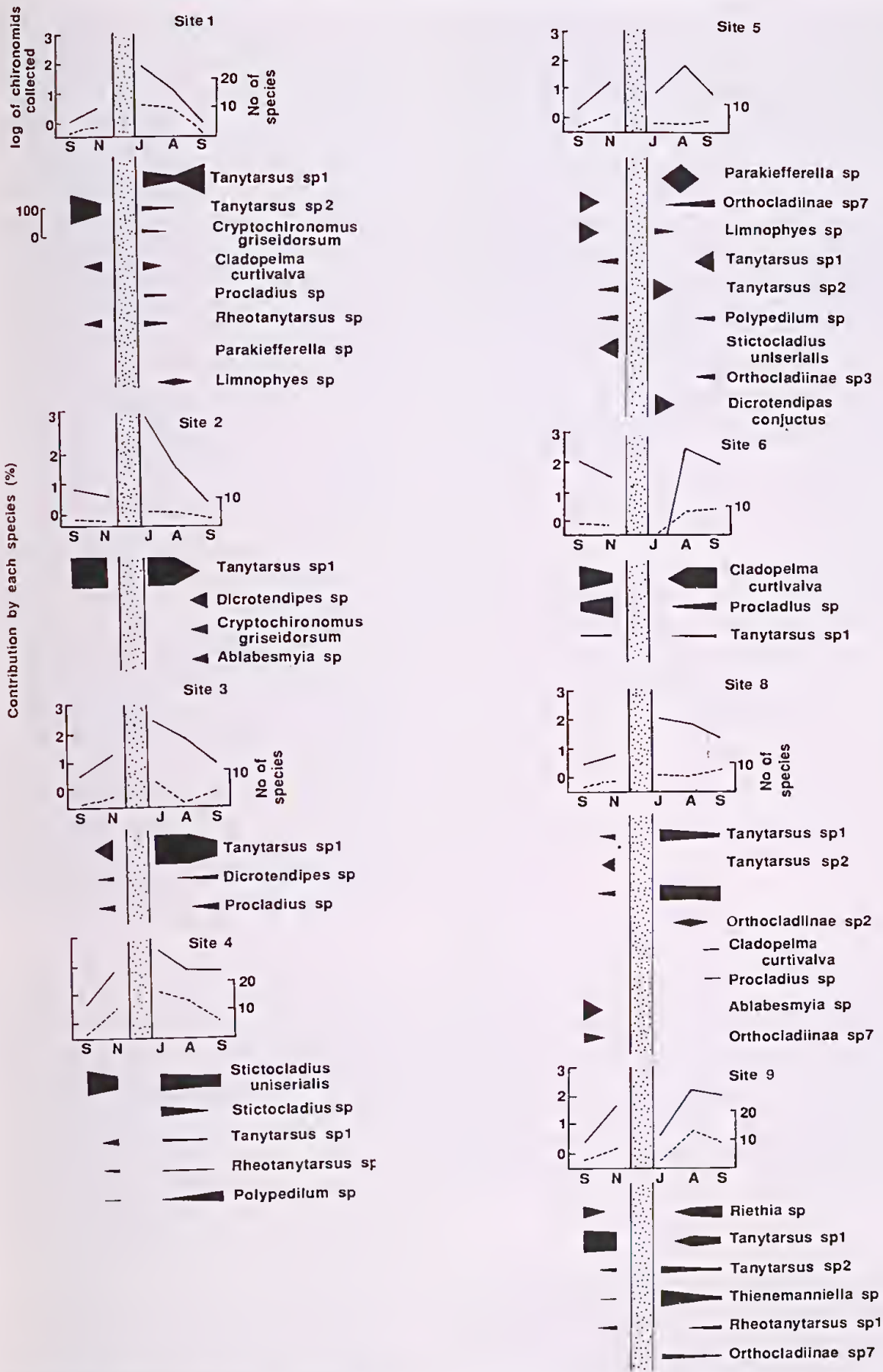


Figure 7 Temporal changes in species richness, abundance and proportional contribution of major species of chironomid larvae at each site.

sites was 64.3%. Site 4 contained a higher proportion of insect taxa (81%); this was not due solely to a paucity of planktonic crustacea (see above) for the number of insect taxa at this site was elevated above all other sites. This site contained the largest number of species of all sites. There was no overall tendency for permanent water sites to have greater numbers of species despite Site 4 having the greatest species richness. For example, Site 6 (a permanent pool) had fewer species than Site 9 and only marginally greater numbers of species than the site with the fewest species (Site 3). If water mites are excluded then differences between pool sites become even less pronounced. The major difference in species number was between permanent and temporary streams (Sites 4 & 5). These streams also shared few species.

Table 7

Between site similarities of species composition determined by Jaccard coefficients. Data listed are the similarity coefficients for the entire fauna, the crustacean fauna and the insect fauna respectively.

1	Site							
	2	3	4	5	6	8	9	
—	0.36 0.45 0.26	0.36 0.47 0.27	0.31 0.50 0.31	0.32 0.44 0.41	0.27 0.57 0.23	0.39 0.62 0.41	0.39 0.44 0.42	
2	—	0.58 0.83 0.28	0.21 0.44 0.12	0.20 0.29 0.15	0.26 0.35 0.24	0.33 0.55 0.22	0.28 0.47 0.19	
3		—	0.22 0.47 0.17	0.29 0.42 0.20	0.25 0.30 0.22	0.36 0.58 0.28	0.29 0.42 0.20	
4			—	0.21 0.27 0.20	0.22 0.36 0.21	0.29 0.53 0.23	0.37 0.53 0.35	
5				—	0.24 0.14 0.18	0.28 0.33 0.23	0.31 0.25 0.31	
6					—	0.25 0.33 0.30	0.33 0.40 0.29	
8						—	0.35 0.47 0.32	

Assemblage similarity, based on presence of shared species, was low for most site comparisons for both the total fauna and the insect fauna (Table 7). Comparisons of crustacean fauna, however, showed a greater similarity especially between sites of close proximity (Sites 2 & 3). Fifty two percent of the insect species collected from the southern acid peat flats have also been collected from lotic waters of the northern jarrah forest (Appendix 1).

Discussion

Water chemistry

Bayly (1964) suggested, on the basis of the distribution of the calanoid copepod, *Calamoecia tasmanica*, that an extensive area of coastal lowland of the southern half of the Australian continent, originally defined by Coaldrake (1961), may have a limnological as well as botanical unity. Bayly (1964) showed that, like many Australian waters, including those of south-western Australia (Williams &

Buckney 1976), the proportions of dissolved ions were more similar to those of seawater than world average freshwater. Sites included in this report also showed, on average, this same ratio of major cations but with a slightly increased dominance by sodium ions. Salinities recorded in the present study are higher than that recorded by Bayly (1964) for dune lakes but much lower than reported for the majority of Western Australian rivers and lakes by Williams & Buckney (1976). It is generally accepted that rainwater salts are derived from the sea and that this source may contribute substantially to coastal freshwaters (Hart & McKelvie 1986). Accumulation of salts during the drying phase of the ephemeral waters of the flats plus an annual delivery via rainfall causes the slight salinization noted here.

The seasonal pattern of change in ionic concentrations is predominantly attributable to the seasonality of the rainfall. Minimum concentrations occur at a time of maximum rainfall and increased concentrations toward summer are associated with reduced rainfall and increased evaporation (Pusey & Edward in press). High concentrations at the beginning of the winter appear not to be related to rainfall *per se* but perhaps rather to elevation of the water table and dissolved salts within the ground water. Substantial dilution by subsequent rainfall would result in the seasonal decrease in salinity observed here. Seasonal variations in dissolved oxygen, temperature and the concentration of major ions, similar to that reported here, also occur in temporary and permanent headwater streams of the northern jarrah forest of south-western Australia (Bunn *et al* 1986). A major difference between the water chemistry of the two areas, however, concerns the timing of fluctuations in pH. Bunn *et al* (1986) found pH to be at its minimum in summer corresponding to periods of reduced flow and peak input and leaching of organic substances from *Eucalyptus* leaf litter. These leached organic compounds are the most likely substances contributing to the acidity of these streams at this time (Bunn pers comm). This contrasts with a late winter low in the study area. A winter low in pH was also recorded in two acidic dune lakes of south-eastern Queensland (Outridge *et al* 1989).

Bayly (1964) considered that in dune lakes, in the absence of appreciable amounts of bicarbonate, organic acids leached from the peaty substrate contribute substantially to acidity. Similarly, the underlying peat may contribute significantly to acidity in the southern acid peat flats. Leaching of organic compounds from submerged leaf litter would also appear to be an important source of acidity. Prolonged inundation, low flows and the flat terrain of the sedgeland would tend to favour the release and retention of such substances. Moreover, as the extent of inundation is determined by rainfall and is hence seasonal in nature, delivery of organic compounds would peak when maximum inundation occurred thus resulting in a late winter low of pH. Because leaching is a rapid process further rainfall would tend to dilute and increase pH.

Similarities in water transparency also exist between the dune lakes of south-eastern Queensland and the waters studied here. Dark stained waters, due to the presence of dissolved organic compounds, are characteristic of "perched" dune lakes and also of coastal streams and swamps of the "wallum" belt of the mainland coastal area

(Endler, Pusey & Arthington unpubl data). The darkest waters of the southern acid peat flats are comparable to the upper limits of G440 determined for Australian waters and tabulated by Kirk (1986) and Bowling (1988) but much lower than recently reported values for some Western Australian wetlands (Wrigley *et al* 1988). It is interesting to note that sites 2 & 3, although similar in many respects to the other sites, have very clear water with low concentrations of dissolved organic compounds. Moreover, these sites have the highest pH of all the sites examined. The more claylike nature of the substrates of these sites may provide an impervious barrier to the transport of organic substances into the water column from the underlying peat, or, peat substrates may be lacking from the soil profile of this particular area. These sites are not fed by streams and the water contained in the pools is a result of direct precipitation (which is retained because of the claylike soil) until maximum inundation of the flats. Only at this time do these sites receive water from the flats. This may explain the erratic changes in ion concentrations at these two sites.

Despite water transparency being greater at site 2, chlorophyll concentrations were not also correspondingly higher as would be expected if light transmittance were a limiting factor for phytoplankton production. Kirk (1986) suggests that this would normally be the case in all but the shallowest waters. All the sites examined here were shallow (< 2 m) and chlorophyll a concentrations were comparable to concentrations recorded in dune lakes (Outridge *et al* 1989) where water transparency may be double that recorded here. Nutrient availability, rather than light, may be responsible for the differences between sites in chlorophyll concentrations. (Site 4, a moderately fast flowing stream, may be an exception as high phytoplankton abundances are not to be expected for lotic environments.) The observation of filamentous algae associated with the substrates of Sites 2 & 3 at a time when phytoplankton densities were low, suggests that nutrients may be limited in the water column because of an interaction between nutrients and inorganic sediments. Barclay (1966) noted that the presence of filamentous alga in a temporary pond occurred only when the pond first filled.

Invertebrate fauna

Many of the common species of microcrustacean fauna recorded here occur in many lentic habitats throughout Australia. *Calamoecia tasmanica* has been recorded from many coastal low altitude freshwater habitats especially those of low salinity and pH (Bayly 1964, 1979, Timms 1970a). Similarly, *Macrocyclops albidus* has also been recorded in eastern Australia (Timms 1967, 1969, 1970a). Cladoceran species recorded from the southern acid peat flats which also show a wide distribution include *Alona affinis* (Shiel 1976, Mitchell & Williams 1982), *Chydorus cf sphaericus* (Morton & Bayly 1977, Shiel 1976, Timms 1967, 1970a, Mitchell & Williams 1982) and *Neothrix armata* (Morton & Bayly 1977, Bayly 1982). It should be noted that *Narmata* and members of the above two genera have all been reared from samples of dry mud (Gurney 1927).

Bayly (1979) recorded the presence of an additional calanoid copepod from waters of the southern acid peat flats. This species, *Calamoecia elongata*, was said to be positively associated with temporary waters and as such

must have some mechanism of drought survival. Such adaptations may also be shared by *C. attenuata* and *C. tasmanica* for they were found in association with temporary waters also and were present shortly after inundation and dominated the planktonic fauna for much of the wet season. Both these species produce large numbers of drought resistant eggs (Pusey unpublished data) and this undoubtedly accounts for their dominance early in the wet season.

As many of the Ostracoda could be identified only to genus, little can be said about the extent of distribution of each species. However, many of the genera recorded are very widespread (Timms 1970a, b, Shiel 1976; Towns 1985; Bunn *et al* 1986). Members of the genera *Ilyodromus* and *Cypretta* are known to be associated with temporary waters (Barclay 1966, Bayly 1982) and one species *Cypretta baylyi* has been recorded from temporary pools of the southern acid peat flats (Bayly pers comm).

It should be emphasized that included in the unpublished data of Bayly (pers comm) for temporary pools in the general vicinity of the present study area are 6 calanoid and 5 cyclopoid Copepoda, 5 Ostracoda and 13 Cladocera of which only 2, 1, 2 (both tentative) and 2 respectively were recorded in this study. Although this study shows relatively high similarity in the composition of each location's microcrustacean assemblage, Bayly's data indicate that there is still considerable heterogeneity between pools.

Despite having widespread distributions, the insect fauna shows less similarity between sites than does the crustacean fauna. This difference is likely a result of the difference in drought survival mechanisms employed by the two groups. Insects, relying on annual recolonization, would tend to show patchy distributions resulting in dissimilar assemblage structure. The Crustacea, in contrast, appear to depend more on drought survival as eggs and thus ensure the continued presence of species between years. Any colonization that might occur would only tend to increase similarity.

Many of the species of Chironomidae, particularly the common species, also have distributions that encompass both south-western and eastern Australia. Several common lentic species with Australia wide distributions and including a number recorded for the southern acid peat flats are known to be opportunistic and colonize a variety of habitats (Edward 1986). Maher & Carpenter (1984) record that several genera and a number of species recorded in the present study were also important components of the benthic fauna of seasonally flooded Murrumbidgee Swamp and Lake Merrimajeel in New South Wales and described them as opportunists. Edward (1986) suggests that opportunism is common in the Chironomidae and that few species, with the exception of members of the genera *Paraborniola* and *Allotrissocladus* (Jones 1975), have drought survival mechanisms.

The only non-crustacean species recorded in the present study that is known to be positively associated with temporary waters is the snail *Glacidorbis occidentalis* (Bunn *et al* 1986). Conspicuously absent from the fauna were species of the crustacean order Anostraca and suborder Conchostraca, both of which are characteristic of temporary waters (Bayly & Williams 1973). Many of the insect species recorded here are present in permanent streams

and rivers of the northern jarrah forest (see Appendix 1) and it appears that few are especially adapted to temporary waters. It seems more probable that an adaptation to the seasonality of rainfall allows these species to colonize temporary waters as if there was little distinction between temporary and permanent waters at this time of the year. In view of this high overlap in species composition it is not unreasonable to suggest that many of the species recorded here and in jarrah forest streams will also occur in streams of the karri forests. It should be noted that the Trichopteran family Philoreithridae, absent from the northern jarrah forest (Bunn & Davies 1989) was present in the southern acid peat flats.

Zooplankton densities, when at their maximum, are comparable to other natural lentic systems, notwithstanding the differences in methods of collection (eg Shiel 1976). They were, however, never as high as those recorded for enriched systems (Mitchell & Williams 1982). The densities of zoobenthos recorded in the present study are almost an order of magnitude higher than densities recorded in headwater streams of the northern jarrah forest (Bunn *et al* 1986).

The decrease in zooplankton and zoobenthos abundance, due mainly to declines in abundance of *Calamoecia* spp. and chironomid larvae, that occurs with increasing pond age corresponds to invasion of these temporary systems by small fish which utilize the southern acid peat flats for spawning (Pusey & Edward 1990). Several studies have shown that fish predation may affect both zooplankton (Geddes 1986, Vanni 1986, Bendall & McNicol 1987, Post & McQueen 1987) and zoobenthic communities (Gilinsky 1984). No fish were recorded from Site 3 in 1986 (Pusey & Edward 1990) and in that year plankton abundance did not decline as markedly with time as at other sites, especially the structurally and chemically similar site 2. Moreover, of all the sites at which *Calamoecia* spp were present, Site 3 was the only one to show an increase in the proportion of these species with increasing age of the pond. *Calamoecia* spp figure prominently in the diets of all the fish species present on the southern acid peat flats (Pusey unpubl data).

High insolation and shallow water depths apparently allow sufficient light penetration to support algal production despite low transmittance. This may be important in maintaining both the planktonic and benthic community especially where the low organic content of the substrate would seem to preclude its importance as a significant source of organic carbon *ie* sites 2 & 3. At sites fed by drainage from the flats, allochthonous input of carbon may be substantial. Given the slight discharge over these areas sufficient time for significant processing by invertebrate shredders may occur. Leaf litter, even after some initial fragmentation (which is unlikely in such low velocity environments), would tend to remain *in situ* until processing by invertebrates was well advanced, at which time only small particles would be removed from the flats by drainage. If this were so then most particulate organic carbon entering streams and ponds would be of the fine fraction. This may explain the low trophic diversity observed for the Chironomidae. Trophic diversity may be higher on the flats themselves because of the probable presence of shredders and because autotrophy may be substantial in shallow areas (Meyer 1986).

Species richness data presented here support the contention that permanent waters have a greater species richness than do temporary waters but also suggests that this effect was limited to the permanent lotic system. Given that major seasonal changes in fauna can occur in streams of south-western Australia (Bunn *et al* 1986) and that permanent waters were sampled during the winter only, the differences in species richness may potentially be higher and apply to permanent pools also.

The number of taxa at any one site is comparable to that of pools and temporary streams of South Australia (Towns 1985) and northern Queensland (Smith & Pearson 1987). These latter authors suggest that species richness in northern Queensland temporary pools is higher than that of temperate regions. As species richness for temporary waters of the present study is greater than that of Smith & Pearson (1987) (104 *vs* 78) doubt is cast on this suggestion. Moreover, the original proposition was based on a comparison with Towns (1977) and there exists a large difference in the number of pools examined by each. As Smith & Pearson (1987) showed that species composition varied greatly between pools, as in this study, the number of pools examined will therefore greatly influence the estimation of overall species richness. It has been suggested that high heterogeneity of species composition in ponds and other small water bodies reflects the highly individual nature of these habitats (Friday 1987). An alternative explanation for the ponds and streams studied here is that differences in the probability of colonization are the main cause of such heterogeneity. This may especially be the case where the habitats as in the present study form a relatively homogenous group with respect to water chemistry and substrate composition.

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Appendix 1

Systematic list of taxa of invertebrates collected from the southern acid peat flats and the study sites in which they were present. An asterisk indicates whether a species is also present in streams and rivers of the northern jarrah forest (Bunn *et al* 1986, Edward unpubl data). Voucher numbers (Aquatic Research Laboratory, UWA) are only included for chironomid larvae identified to family or genera.

Taxon	1	2	3	4	5	Site 6	8	9
Mollusca								
<i>Glacidorbis occidentalis</i> *					X			
<i>Ferrissia pettardi</i> *						X		
<i>Physastra</i> sp								X
Annelida								
Oligochaete	X	X	X	X	X	X	X	X
Arachnida								
<i>Oribatida</i> sp 1		X			X	X		
<i>Oribatida</i> sp 2								X
<i>Oribatida</i> sp 3					X	X		X
Bdellidae sp					X			
<i>Mesostigmata</i> sp					X			
undescribed species and genera						X		X
<i>Limnesia</i> sp		X	X					
<i>Oxus</i> sp						X		X
<i>Arrenurus</i> sp								X
<i>Coaustraliobates</i> sp						X		
<i>Koenikea</i> sp						X		
Crustacea								
Ostracoda								
<i>Ilyodromus</i> sp 1	X					X		
<i>Ilyodromus</i> sp 2		X	X				X	
<i>Ilyodromus</i> sp 3		X	X					
<i>Ilyodromus</i> sp 4							X	
<i>Gomphodella</i> sp		X	X			X		
<i>Cypretta</i> sp		X	X	X				X
<i>Newhamia</i> sp		X						
<i>Limnocythere mowbrayensis</i>		X	X	X	X		X	X
<i>Limnocythere</i> sp					X			
undescribed genera					X			
Copepoda								
Harpacticoidea sp 1	X	X	X		X	X	X	X
Calanoidea								
<i>Calamoecia (attenuata & tasmanica)</i> *	X	X	X	X	X		X	X
Cyclopoidea								
<i>Macrocyclops albidus</i> *	X			X		X		
<i>Metacyclops</i> sp (cf <i>arnaudi</i>)	X	X	X	X	X	X	X	X
Cladocera								
<i>Alona (=Biapertura) affinis</i>	X	X	X	X		X	X	X
<i>Echinisca</i> sp (cf <i>capensis</i>)	X	X		X		X	X	X
<i>Neothrix armata</i>	X	X	X		X		X	
<i>Simocephalus acutirostratus</i>	X		X	X	X		X	
<i>Chydorus</i> sp	X	X	X			X	X	X
Isopoda								
Phreatoicoidea								
<i>Amphisopus ?lintoni</i>		X	X		X			
<i>A. ?annectans</i>					X			
Amphipoda								
<i>Perthia acutitelson</i> *						X		
<i>Perthia</i> sp 1		X	X	X			X	
<i>Perthia</i> sp 2	X	X	X	X			X	
undescribed genera					X			
Decapoda								
<i>Cherax ?plebejus</i> *	X	X	X	X	X	X	X	X

Appendix 1—continued

Taxon	Site								
	1	2	3	4	5	6	8	9	
Insecta									
Collembola									
<i>Sminthurides ?stagnalis</i>	X	X	X	X	X	X	X	X	X
<i>Xenylla</i> sp		X			X	X		X	
<i>Brachystomella</i> sp	X			X			X		
<i>Isotoma</i> sp		X			X	X	X		
Odonata									
Lestidae sp		X							
Ephemeroptera									
<i>Bibulmena kadjina</i> *	X			X				X	
<i>Nyungara bunni</i> *	X			X				X	
Plecoptera									
<i>Newmanoperla exigua</i> *	X	X							
<i>Leptoperla australica</i> *				X			X		
Trichoptera									
Leptoceridae									
<i>Lectrides parilis</i> *						X			
<i>Triplectides</i> sp B*					X			X	
<i>Oecetis</i> sp*				X		X			
<i>Notalina</i> sp*								X	
<i>Notalina</i> sp A*								X	
<i>Symphytoneuria</i> sp 1								X	
<i>Symphytoneuria</i> sp 2	X	X				X			
Leptocerid sp 1				X					
Hydroptilidae									
<i>Acroptila ?globosa</i> *						X			
<i>Oxyethira</i> sp*	X				X		X		
<i>Hellyethira / Acritoptila</i> sp	X		X		X	X	X	X	
<i>Hellyethira</i> sp B*			X			X		X	
<i>Maydenoptila</i> sp A*					X				
<i>Maydenoptila</i> sp							X		
Ecnomidae									
<i>Ecnomina ?trulla</i> *				X					
<i>Ecnomus pansus</i> *						X			
Ecnomidae sp				X					
Philoreithridae									
<i>Kosrheithrus</i> sp				X					
Hemiptera									
<i>Diaprepocoris</i> sp		X	X				X		
<i>Notonecta</i> sp		X	X						
Coleoptera									
<i>Sternopriscus browni</i> *	X	X	X	X	X	X	X	X	
<i>S. marginatus</i> *				X					
<i>S.</i> sp 1		X	X					X	
<i>Homeodytes scutellaris</i> *		X	X						
<i>Rhantus suturalis</i> *			X		X				
<i>Uvarus pictus</i> *		X			X				
<i>Antiporus</i> sp*		X							
Helodidae sp*		X							
Hydrophilidae sp 1*		X							
Hydrophilidae sp 2						X			
Curculionidae sp 1			X				X		
Curculionidae sp 2							X		
Diptera									
Simuliidae									
<i>Austrosimulium funosum</i> *	X			X	X			X	
<i>Austrosimulium</i> sp A.x*	X			X	X			X	
? <i>Cnephia</i> sp 1*				X	X				
? <i>Cnephia</i> sp 2*				X	X				
Ceratopogonidae									

Appendix 1—continued

Taxon	Site								
	1	2	3	4	5	6	8	9	
sp A*				X		X		X	
sp F				X		X	X	X	
sp G		X	X	X		X		X	
Tipulidae									
<i>Limnophila</i> sp				X					
Muscidae									
<i>Limnophora</i> sp	X			X					
Culicidae									
<i>Anopheles</i> sp		X	X		X	X			
<i>Aedes</i> sp	X	X	X						
Empididae				X					
Dolichopodinae				X					
?Sciomyzidae				X					
Chironomidae									
Tanypodinae									
<i>Paramerina levidensis</i> *	X	X		X			X	X	
<i>Paramerina</i> sp (cf <i>levidensis</i>)[SW6]	X	X		X		X	X	X	
<i>Macropelopia dalyupensis</i>						X			
<i>Ablabesmyia</i> sp [SW25]		X				X	X		
<i>Procladius</i> sp [SW12]	X	X	X	X	X	X			
Aphroteniinae									
<i>Aphroteniella filicornis</i> *				X					
<i>Aphroteniella</i> sp [SW21,?V30]*	X								
Orthoclaadiinae									
<i>Stictocladius uniserialis</i> *	X			X	X			X	
<i>Stictocladius</i> sp [SW32]				X					
<i>Cricotopus annuliventrus</i> *				X					
<i>Thienemaniella</i> sp [V19]				X				X	
<i>Limnophes</i> sp	X			X	X	X	X		
<i>Parakiefferiella</i> sp [V5C9]*	X		X	X	X		X	X	
Orthoclaadiinae sp 1 (cf <i>Limnophes</i>) [SW7]	X						X	X	
sp 2 (cf <i>Limnophes</i>) [V31]*				X		X			
sp 3 [SW23]					X				
sp 4 [SW28]				X					
sp 5 [SW29]				X					
sp 6 [SW30]				X					
sp 7 [VCD2]	X				X		X	X	
Chironominae									
<i>Cryptochironomus griseodorsum</i> *	X	X		X			X	X	
<i>Chironomus</i> aff. <i>alternans</i> *		X							
<i>Dicrotendipes conjunctus</i> *		X	X		X				
<i>Dicrotendipes</i> sp [V47]	X	X	X			X	X	X	
<i>Cladopelma curtivalva</i> *	X		X	X		X	X		
<i>Cladopelma</i> sp [SW26]							X		
<i>Kiefferulus martini</i>							X		
<i>Polypedilum</i> sp A [V3]*				X		X	X	X	
<i>Polypedilum</i> sp B [V33]*	X		X	X	X				
<i>Riethia</i> sp 1 [V4]*				X				X	
<i>Riethia</i> sp 2 [V5]*								X	
<i>Harnischia</i> sp [VCD10]*				X					
<i>Paratendipes</i> sp [V12]*						X			
<i>Tanytarsus</i> sp 1 [SW2]*	X	X	X	X	X	X	X	X	
<i>Tanytarsus</i> sp 2 [SW3]*	X		X	X	X		X	X	
<i>Rheotanytarsus</i> sp 1 [SW10]*			X	X				X	
<i>Rheotanytarsus</i> sp 2 [SW20]	X			X	X	X		X	
<i>Stempellina</i> sp [V7]*	X	X							